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1 **The article category: Review Article**

2 **Title: Sexual reproduction and diversity: connection between sexual selection and biological**
3 **communities via population dynamics**

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9

10 **Abstract:** Sexual reproduction is a mysterious phenomenon. Most animals and plants invest in
11 sexual reproduction, even though it is more costly than asexual reproduction. Theoretical studies
12 suggest that occasional or conditional use of sexual reproduction, involving facultative switching
13 between sexual and asexual reproduction, is the optimal reproductive strategy. However, obligate
14 sexual reproduction is common in nature. Recent studies suggest that the evolution of facultative
15 sexual reproduction is prevented by males that coerce females into sexual fertilization; thus, sexual
16 reproduction has the potential to enforce costs on a given species. Here, the effect of sex on
17 biodiversity is explored by evaluating the reproductive costs arising from sex. Sex provides atypical
18 selection pressure that favors traits that increase fertilization success, even at the expense of
19 population growth rates, i.e., sexual selection. The strength of sexual selection depends on the
20 density of a given species. Sexual selection often causes strong negative effects on the population
21 growth rates of species that occur at high density. Conversely, a species that reduces its density is
22 released from this negative effect, and so increases its growth rate. Thus, this negative density-
23 dependent effect on population growth that arises from sexual selection could be used to rescue
24 endangered species from extinction, prevent the overgrowth of common species, and promote the
25 coexistence of competitive species. Recent publications on sexual reproduction provide several

26 predictions related to the evolution of reproductive strategies, which is an important step towards
27 integrating evolutionary dynamics, demographic dynamics, and community dynamics.

28

29 **Keywords:** biological community; intraspecific competition; density dependence; population
30 dynamics; sexual selection

31 Why sexual reproduction is widespread in animals and plants remains a long-standing mystery
32 in evolutionary ecology. Sex is associated with numerous short-term costs that asexual organisms
33 mostly avoid (Maynard Smith 1971; Williams 1975; Bell 1982; Lehtonen et al. 2012). Theoretical
34 studies have demonstrated that investing in small quantities of sexual reproduction represents the
35 optimal reproductive strategy in predominantly parthenogenetic organisms (Charlesworth et al. 1993;
36 Green and Noakes 1995; D'Souza and Michiels 2010). However, obligate sex is the dominant
37 reproductive system in nature. Therefore, the mystery of sex is the prevalence of obligate sexual
38 reproduction (Burke and Bonduriansky 2017). Recent studies have provided the notable hypothesis
39 that males force asexual females to reproduce sexually (Dagg 2006; Kawatsu 2013b, a, 2015), which
40 is a very simple but powerful solution for the mystery of sex. Males cannot reproduce by themselves
41 without sexual reproduction, so they must forcibly mate with females, even if coercion is required.
42 Consequently, facultative and obligate asexual reproduction are removed from the population. If this
43 scenario is correct, the various costs of sexual reproduction arise from forced mating by males. This
44 type of selection pressure that arises from sexual reproduction has been documented since Darwin's
45 era, because males often have traits that are useless for survival, but beneficial for mating. This
46 pressure is named sexual selection to distinguish it from natural selection (Darwin 1859, 1871). If the
47 evolutionary dynamics driven by the sexual selection affect the population growth rates of sexual
48 organisms, this effect of sexual selection must influence a broad range of biological communities,
49 because sexual reproduction is common in eukaryotes. However, just as the effects of sexual
50 selection have long been overlooked in the context of the mystery of sex, they have not been
51 adequately explored in biological communities. Thus, in this review, I discuss two hypothetical
52 mechanisms, in which sexual traits regulate population dynamics, along with suggestion of
53 remaining problems and potential experimental approaches that could be used to test model
54 predictions of the hypotheses.

55 One of the greatest challenges in ecology is elucidating the conditions under which biodiversity

56 may sustained over long timeframes (Tilman 2000). Self-regulation mechanisms of population size
57 are known as fundamental to sustain ecological communities (May 1972; Yodzis 1981; Barabás et al.
58 2017; Gavina et al. 2018). These mechanisms are achieved by a negative density-dependent effect
59 (NDDE) on population growth rates. If an NDDE exists, the density of species with low densities
60 will increase, which prevents extinction. In comparison, overgrowth is prevented in species with high
61 densities. An NDDE is generally explained by two mechanisms: predation pressure from natural
62 enemies (Elton 1927; Murdoch 1969) and intraspecific competition for resources (Gause 1934;
63 Macarthur and Levins 1967). Recently, the importance of sexual selection on population dynamics
64 has been pointed out (Kokko and Brooks 2003; Kokko and Rankin 2006; Kobayashi 2018). NDDE
65 arising from sexual selection results from competition for mating or fertilization success. At high
66 densities, where strong mating competition is expected, sexual selection favors traits that increase
67 mating success, even at the expense of population growth rates. In contrast, at low densities, this
68 negative effect on growth rate is mitigated, because there is less competition for mating in rare
69 species. Thus, the coexistence of many competitive species becomes possible, because sexual
70 selection has the potential to control the reproductive rate of any sexual species. This mechanism is
71 similar to the resource competition mechanism, because both arise from intraspecific interactions.
72 However, when considering niche theory, these mechanisms differ slightly, because sexual selection
73 promotes coexistence without niche partitioning between species. Given the biological species
74 concept, which defines species as groups of interbreeding natural populations that are reproductively
75 isolated from other groups (Mayr 1970), mating competition must occur within a given species;
76 consequently, sexual selection works depending on the density of each species. Therefore, even if
77 competitive species share the same niche space, the NDDE arising from sexual selection allows them
78 to coexist stably, as long as the biological species concept holds and the mechanisms arising from
79 resource competition do not. This case will be rare under natural conditions, because niche
80 differentiation is favored by the natural selection of competitive species to reduce competition for

81 resources.

82

83 The first example that causes NDDE related to sexual reproduction is sex allocation. The most
84 renowned sex allocation theory predicts equal allocation to male and female reproductive functions
85 for the optimal division of resources (Fisher 1930). Because of this allocation, the production of
86 males is considered as one of the largest costs of sex (Maynard Smith 1971; Lehtonen et al. 2012).
87 However, equal allocation occurs under certain conditions, such as random mating and large mating
88 populations. In situations where sons compete with each other for mating partners in a local
89 population, the allocation to sons (or male functions, such as pollen in plants) reduces the mating
90 success rate for each son, because strong mating competition occurs among sons for a limited
91 number of mating partners. In comparison, greater allocation to daughters creates more mating
92 partners for the sons. This situation is called local mate competition and was modeled by Hamilton
93 (1967). In this model, the evolutionarily stable allocation to females is $(n + 1)/2n$, where n represents
94 the number of mothers in a local mating population. When n is sufficiently large, equal allocation
95 (0.5) occurs. In contrast, if a single mother is present in the local mating population ($n = 1$), this
96 female should allocate most of its resources to daughters. Thus, this intraspecific competition for
97 mating promotes the evolution of highly female-biased allocation, depending on the number of
98 mothers in the local mating population (Hamilton 1967; West 2009). Because the allocation to
99 females is strictly linked to the population growth rate, adaptive sex allocation results in an NDDE
100 on population growth, leading to the stable co-occurrence of competitive species (Hassell et al. 1983;
101 Zhang and Jiang 1995; Kobayashi and Hasegawa 2016; Kobayashi 2017). Models that incorporate
102 this mechanism have demonstrated that hundreds of species can co-occur over 10,000 generations
103 even in homogeneous environments, recreating the observed patterns of biodiversity (Kobayashi
104 2017). This study (Kobayashi 2017) clearly showed that sexual reproduction has the potential to
105 influence the ecological community via the evolutionary dynamics of sex allocation. At present, it is

106 not clear whether this mechanism works well under natural condition. Recent eco-evolutionary
107 feedback studies demonstrate the importance of genetic variation (Pelletier et al. 2009; Post and
108 Palkovacs 2009). However, there is insufficient information about genetic variation related to sex
109 allocation at the population level. The exception is haplodiploid species that can alter sex allocation
110 without genetic difference by controlling fertilization. Some wasps under the condition of local mate
111 competition theory are able to adequately alter their sex allocation, depending on the number of
112 competitors (Werren 1983; Herre 1985). Thus, hymenopteran species that exhibit local mate
113 competition could be good material to test the relationship between NDDE and sex allocation.

114 Another example is sexual harassment, which is a trait of one sex (usually male) that increases
115 its fertilization success rate but reduces the fecundity of its mating partners. Although previous
116 empirical studies have provided evidence of the density or frequency dependence of sexual selection
117 (Andersson 1994; Levitan 2004; Gosden and Svensson 2009; Takahashi and Kawata 2013), the
118 relationship between the density dependence of sexual selection and population growth rate remains
119 obscure (Kokko and Brooks 2003; Kokko and Rankin 2006), but see also (Mikami et al. 2004;
120 Takahashi et al. 2014). Sexual harassment creates an NDDE similar to that resulting from sex
121 allocation. For high-density species, sexual selection favors males that utilize strong harassment to
122 increase their fertilization success rate, even at the expense of the fecundity of their mating partners.
123 At low densities, which means fewer competitors are present, such too strong harassment becomes
124 disadvantageous for the harasser, because it decreases the fecundity of the mating partners despite
125 the fertilization success is secured to some extent without harassing; therefore, sexual selection
126 generally has an NDDE on the population growth rate of sexual organisms. This situation was
127 modeled in a recent study, which also revealed that sexual harassment has an NDDE on the
128 population growth rate, promoting the stable co-occurrence of competitive species (Kobayashi
129 2018). Thus, as shown by the model of sex allocation (Kobayashi 2017), this recent study
130 demonstrated that the evolution of sexual harassment reduces the fecundity per individual, depending

131 on the density, allowing hundreds of species to co-occur without niche differences.

132 Both of these examples show that sexual organisms, generally, have the ability to self-regulate
133 the size of their populations. Of note, these two mechanisms generate slightly different population
134 dynamics from the time-scale perspective. In the case of sex allocation, a change in the abundance of
135 each species promotes an evolutionary change in sex allocation, and vice versa. Thus, NDDE arising
136 from sex allocation takes time, because a change is required in the average sex allocation depending
137 on genetic variation and mutations within the species. Because small populations have low
138 evolutionary potential (few genetic variations within populations and low mutation rates per
139 generation at the population level), relatively rare species tend to show greater variation in
140 population dynamics than common species (Fig. 1a). In the sexual harassment models, when
141 abundance increases, the numbers of copulation, courtship and pollinated pollen grains increase;
142 consequently, the amount of harassment to which each individual is subjected increases immediately
143 without any evolutionary processes, and vice versa. Because NDDE arising from sexual harassment
144 does not require evolutionary change, and mostly depends on the abundance of a given species,
145 sexual harassment models show relatively stable population dynamics (Fig. 1b). These two
146 mechanisms are not mutually exclusive. Further research is required to clarify the dynamics that
147 occur when both of these mechanisms occur simultaneously.

148 Harassment models suggest that flowering plants represent ideal model systems in future
149 research on this topic. Compared with animals, it is difficult for plant species to interact directly with
150 other conspecific individuals; consequently, most sexual harassment will occur in the pistils, where
151 pollen and pistils directly interact. Thus, competition between pollen tubes in pistils could be used to
152 explore mechanism of harassment (Prasad and Bedhomme 2006; Lankinen et al. 2016). Sexual
153 selection favors pollen traits to ensure fertilization success, even at an expense of some seeds from
154 the pistils. Thus, artificial pollination experiments could prove useful for clarifying the validity of
155 assumptions in modelling the effect of reducing seed production in parallel to increasing pollen grain

156 number on a stigma. Moreover, the model predicts that the optimal strength of harassment depends
157 on the number of competitors; thus, it is important to obtain information on the density of
158 conspecific individuals in sexual organisms. As direct interactions are restricted in plants, it is more
159 difficult for plants than animals to detect density, due to the lack of eye-like sensors. A stigma of a
160 flowers represents important sensor that could be used to detect the density of conspecific
161 individuals, because it can detect the presence of pollen grains on the surface. Thus, the traits of
162 pollen and flowers might change depending on the numbers of pollen donors and pollen grains after
163 pollination. Therefore, the artificial pollination experiments could provide a way of elucidating the
164 evolution of sexual harassment in plant species.

165 Various sexual traits are considered to evolve depending on density, which, in turn, impact
166 population dynamics (Kokko and Brooks 2003; Kokko and Rankin 2006). These traits evolve at the
167 same time, due to density fluctuation, even if the traits have independent genetic bases. Some of
168 these traits might improve population growth, as opposed to sexual harassment. Thus, it is important
169 to consider multiple sexual traits to clarify the generality of NDDE arising from sexual selection, and
170 to obtain an accurate interpretation of the effect of sexual selection on the biological community.
171 Next I explore three situations that several traits could evolve simultaneously.

172 There are many options to remove the negative effects of harassment (e.g., escape, physical
173 rejection of mating and physiological tolerance); however, these options are qualitative, making it
174 difficult to construct analytic models that can be applied to real organisms. One possible counter-
175 strategy for female is the evolution of tolerance to harassment, which reduces the effect of
176 harassment at the expense of reproductive cost. However, knowledge on the efficiency of tolerance is
177 required (reduction of harassment effect per reproductive cost). Studies of efficiency in real
178 organisms would be an interesting topic to explore in evolutionary biology, but might not be
179 important in community ecology because sexual harassment causes NDDE, even when the evolution
180 of tolerance is considered. Although evolutionary optimal tolerance is obscure, whenever the

181 evolution of a counterstrategy improves the fecundity of females, a given species must increase its
182 density. As a result, individuals would be subject to stronger harassment, depending on their
183 abundance. Thus, from the perspective of community ecology, models that incorporate the evolution
184 of tolerance should provide qualitatively similar results, due to the effect of NDDE.

185 Similarly, mate choice should evolve as a counterstrategy to harassment, which might reduce the
186 number of mating partners, leading to a decline in harassment. One of the simplest processes to reject
187 a part of pollen is the evolution of self-incompatibility. Removing harassment from self-pollination is
188 beneficial when harassment is strong. Thus, self-incompatibility might be adaptive when density is
189 sufficiently high, which is intuitive and easy to understand. High-density causes the fecundity of
190 females to decrease, because of male-male competition causing fertilization success rates to decline.
191 Therefore, securing seed production by an individual via the elimination of self-harassment becomes
192 relatively important. Evolution in the opposite direction, from self-incompatible to self-compatible at
193 low densities, is also explained by the model, which is similar to the classical argument that self-
194 compatible is adaptive because of reproductive assurance when pollinators or mates are scarce
195 (Darwin 1876; Tsuchimatsu et al. 2010). Around the density where the optimal strategy switches
196 between self-compatible and incompatible, the evolution of a mixed strategy might support a smooth
197 transition between them. Even when considering these transitions, sexual selection consistently
198 causes NDDE because models assuming both reproductive systems show NDDE(Kobayashi 2018).
199 Therefore, when considering the transition of mating systems, sexual selection has the potential to
200 cause NDDE consistently.

201 Other potential traits influencing population growth rates related to sexual selection exist in
202 animals, such as infanticide by males, paternal brood care, and nuptial gifts. The first example,
203 infanticide, occurs when an immigrating male encounters a mature female with siblings (Swenson et
204 al. 1997), which affects population growth rate depending on density (Moller 2004). The others are
205 cooperative behaviors of males to females and might improve the population growth rates of a given

206 species. Thus, the density dependence of these various options related to sexual reproduction and
207 mating must be considered to clarify the relationship between sexual selection and population
208 dynamics in actual communities.

209 Sexual selection theory has made a number of fundamental contributions to evolutionary
210 ecology; however, its impact on biological communities remains poorly understood. Compared to
211 tests of hypothetical mechanisms that explain the sustainability of biodiversity at the community
212 level, it is easy to explore how strongly NDDE arising from sexual harassment affects the population
213 dynamics of a certain species. By assimilating information on the conditions required for NDDEs in
214 various organisms, we might be able to ascertain when and how the stability of a given biological
215 community and ecosystem collapses. Thus, multiple disciplines of ecology must be integrated,
216 including behavioral ecology, population ecology, and community ecology, to conduct appropriate
217 experiments that clarify the properties of individual species stabilizing an ecosystem. When
218 considering the generality of sexual reproduction in nature, sexual selection theory represents a
219 central topic in multi-discipline ecology. I hope this perspective will stimulate and contribute to the
220 further development of ecology.

221

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227

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- 327
- 328 Figure legends:
- 329 Figure 1.
- 330 Simulation results showing the demographics and evolutionary dynamics. Each plot shows 10

species co-occurrence over 2,000 generations by the evolutionary dynamics of **a** sex allocation and **b** harassment. Each colored line corresponds to the dynamics of each species and starts from approximately **a** 10^5 individuals with equal allocation (0.5), and **b** 10^6 individuals with no harassment (relative productivity = 1). The number on each colored line indicates the amount of available resources for the species. Using the data for **a** is the same with figure 1 in Kobayashi 2017, and for **b** the same with figure 2 in Kobayashi 2018, respectively. The x axis of **b** indicates productivity compared with no sexual harassment, which was decreasing due to evolution of harassment.